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The first Pacific insular orchid bee (Hymenoptera, Apidae): A new species of *Eufriesea* from the Islas Marías

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Abstract

A new species of the orchid bee genus *Eufriesea* Cockerell (Apidae: Apinae: Euglossini) is described and figured from the Islas Marías of Nayarit State, México in the Pacific. *Eufriesea insularis* **sp. nov.**, is a member of the *coerulescens* species group and is restricted to Islas Marias. The species is readily recognized by its dark blue integument with purple iridescence, black pubescence, dark wings, and clypeus green with purple hues and a prominent elevated ridge along the midline. The new species is known only from the female.

Resumen

Se describe e ilustra una especie nueva de abeja de las orquídeas del género *Eufriesea* Cockerell (Apidae: Apinae: Euglossini) de las Islas Marías en el estado de Nayarit, en el pacífico de México. *Eufriesea insularis* **sp. nov.** es parte del grupo de especies *coerulescens* y está restringida a las Islas Marías. La especie se reconoce fácilmente por su integumento azul oscuro con brillos púrpuras, pubescencia negra, alas oscuras y el clípeo verde con brillos púrpura y con un borde elevado a lo largo de la línea media. La nueva especie se conoce únicamente de la hembra.

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Keywords
Anthophila, Apoidea, Euglossini, México, new species, orchid bees

Introduction

The purpose of this paper is to describe a new species of the orchid bee genus *Eufriesea* Cockerell (Apidae: Euglossini) from the Pacific islands of Islas Marías, an archipelago consisting of four islands located 100 km from the coast of the state of Nayarit in México. This archipelago was designated as the Islas Marías Biosphere Reserve in 2010 by UNESCO and the Mexican Government, and it is currently under the protection of the Ministry of the Environment and Natural Resources of México (SEMARNAT-CONANP). We have been aware of the novelty of this species for more than a decade (Ayala and Engel 2008; Gonzalez et al. 2017), but it was awaiting description because of the limited number of available specimens. The new species was initially known to us from two females captured during an expedition led by the Instituto de Biología of the Universidad Nacional Autónoma de México (UNAM) in the mid-1980s on the island of María Madre (Fig. 1), the largest of the four islands and which housed a federal prison, established in 1905 and closed in 2019. Two additional females captured in the mid-1990s on the same island were located at the insect collection of the Universidad de Guadalajara. Unfortunately, appraisal of museum specimens in other Mexican collections as well as in U.S. institutions has not yielded additional material and further sampling on the island has not been possible.

Eufriesea consists of about 60 species confined to the Neotropical region, most of which occur in South America (Ramírez et al. 2002). These bees are readily recognized by their large, robust body with frequently metallic coloration that ranges from black to blue or green with yellow, reddish, or purple iridescence. The genus, like its relatives in the tribe Euglossini, is also noteworthy for its role in pollination of orchids and many other plants, such as those in the families Bignoniaceae (*Allamanda* L., *Astianthus* D.Don, *Melloa* Bureau, *Tecoma* Juss., *Tabebuia* Gomez), Convolvulaceae (*Ipomoea* L.), Fabaceae (*Senna* Mill.), and Apocynaceae (*Thevetia* L., *Cascabela* Raf., *Stemadenia* Benth., *Prestonia* R.Br.) (records from specimens in the Chamela bee collection and personal observations). Males visit orchid flowers, among others, to collect essentials oils that are then carried and modified in their metatibiae, and which are presumably used to attract females (e.g., Moure 1965, Dressler 1967, 1968a, 1968b; Kimsey 1980, 1982; Roubik and Hanson 2004; Michener 2007).

The new species documented here belongs to the *coerulescens* species group, which was recently revised by Gonzalez et al. (2017). This species group consists of six species presumably restricted to México along tropical dry forests, as well as in pine and oak forests, from sea level to about 1500 m in elevation. *Eufriesea coerulescens* (Lepeletier de Saint Fargeau), the most widespread species of the group, has also been recorded from the Guadalupe Mountains of western Texas and southeastern New Mexico, USA (Griswold et al. 2015). Records of this species from Honduras, Costa Rica, and Panama

remain to be confirmed (Gonzalez et al. 2017). We hope that this contribution brings this species to the attention of melittologists and encourages further work on the biology of this isolated orchid bee.

Materials and methods

Morphological terminology for the description follows that of Michener (2007), Engel (2001), and Engel et al. (2021), with the abbreviations T and S for metasomal tergum and sternum, respectively. Illustrations were made using a Canon 7D digital camera and a 60 mm Canon macro lens. The images were stacked using the HeliconFocus program and edited with Affinity Photo. The species description is based on the holotype and paratypes available to us and emphasizes structural characters that are reliable for species recognition in the female, such as length of the glossa, punctation and pubescence of the mesoscutellum, metasomal terga, and tegula; shape of the posterior subapical projection and width of the distal interspur depression of the metatibial proventral surface; and width of the metabasitarsus. Measurements were taken with an ocular micrometer on a Leica MZ6 stereomicroscope and are in millimeters with the variation in size across the type series in parentheticals (n = 4). Intertegular distance was measured as the shortest distance between the mesal margins of the tegulae, while the forewing length was measured from the posterior margin of the tegula to the wing tip. Type material is deposited in the Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, México (**IBUNAM**) and the Colección Entomológica, Centro Universitario de la Costa Sur, Universidad de Guadalajara, Autlán Jalisco, México (**CUCSUR**).

Systematics

Genus *Eufriesea* Cockerell, 1908

***Eufriesea insularis* sp. nov.**
https://zoobank.org/39D3AB9E-7A79-4518-8C45-9F2EB023E0A8
Figs 2–7

Diagnosis. The new species is similar in appearance to other species in the *coerulescens* group, but with a noticeably darker integument with blue and purple iridescence and generally with black pubescence (Figs 2, 3), but yellowish to black on TIV–VI (Figs 2, 5), all of which contrasts with *E. oliveri* Gonzalez and Griswold and *E. micheneri* Ayala and Engel in which such setae are whitish. In addition, the new species has the glossa long, extending beyond SII (Fig. 2); the head, labrum, and clypeus metallic greenish but purple on the discal area of the latter (Fig. 7), and contrasting with the dark metallic blue of the rest of the head; the clypeus has strong elongate punctures that converge towards the midline, and which are stronger than those present on the bordering par-

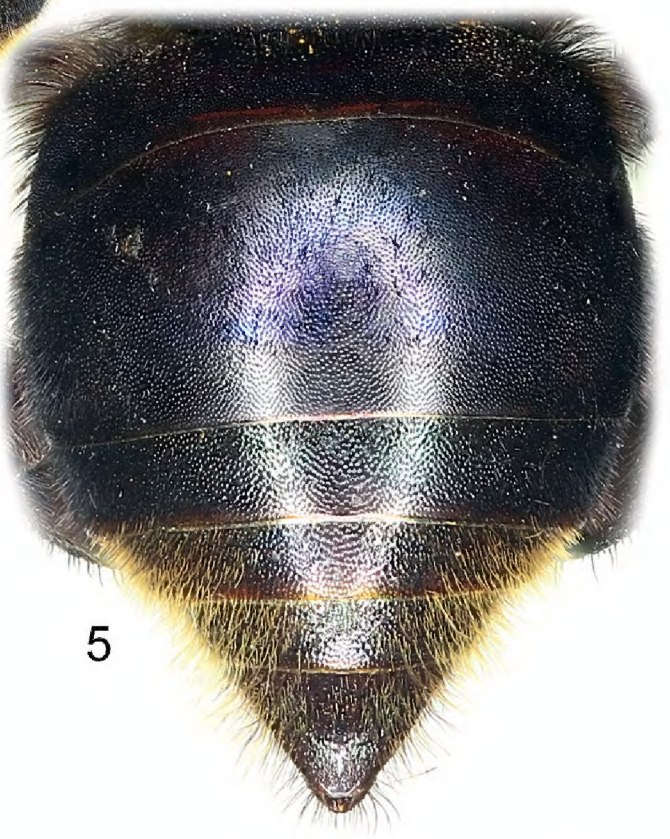
Figure 1. Geographical location of the Marías Islands in the Pacific Ocean, off the coast of Nayarit, México. María Madre Island is the type locality of *Eufriesea insularis* sp. nov.

aocular area; the clypeus has a prominent mediolongitudinal ridge, strongest in apical half of the clypeus (Fig. 7); frons doubly punctate, the largest punctures separated by about their diameter, between the small and large punctures the integument is smooth and shiny; exceptionally narrow impunctate and shiny area between torulus and inner ocular margin, width about one-fifth torular diameter; scape dark reddish brown, flagellum dark brown to nearly black, but flagellomeres I, II, and apical flagellomeres darker (Fig. 7); pronotum partially dark brown, and lateral margins of mesoscutum, axilla, and mesoscutellum dark brown to nearly black (Fig. 6); forewing hyaline and infumate throughout although darker in costal cell, along anterior margin of marginal cell (particularly apically), and slightly so in first submarginal cell (Fig. 3); lighter patch in second medial cell (Fig. 3); femora, metatibia (corbicula), and metabasitarsus dark brown to nearly black in some areas (Figs 2, 4).

Description. ♀: Total body length 19.5 mm (19.5–19.9 mm). Head wider than long, length 5.4 mm (vertex-margin of clypeus) (5.4–5.7 mm), width 6.6 mm (6.5–6.6 mm); compound eye length 4.6 mm (4.6–4.8 mm), width 2.2 mm (2.1–2.2 mm); upper interorbital distance 2.7 mm (2.6–2.9 mm), lower interorbital distance 3.3 mm (3.3–3.5 mm), interorbital distance at tangent of upper third of compound eye length 3.6 mm (3.5–3.6 mm); glossa long, extending beyond SII, length 12.2 mm (12.2–12.6 mm); mandible black and robust, width at base 1.5 mm (1.5–1.6 mm), length 2.4 mm (2.4–2.5 mm); apical tooth largest, projecting beyond medial tooth, forming

Figure 2. *Eufriesea insularis* sp. nov., female holotype (IBUNAM RA 292), lateral habitus.

an orthogonal notch between teeth; labrum with coarse irregular punctures, with short elevated medial carinae, larger than sublateral carinae, sublateral carinae converging apically; distal extreme of labrum with subapical depression and distally and distal margin prominently covered with short pubescence; clypeus with elongate punctures (Fig. 7) that converge towards midline, such punctures stronger than those on remainder of face, integument between punctures shining, finely and microscopically imbricate, with prominent elevated medial ridge (Fig. 7); impunctate and shiny area between toruli and inner margin of compound eye, area between torulus and eye exceptionally narrow, about one-fifth torular diameter; frons doubly punctate, largest punctures separated by about their diameter, integument between punctures smooth and shiny; frontal line well defined between torulus and anterior margin of median ocellus (1.55 mm, 1.53–1.67 mm long); supraclypeal area with impunctate line extending to clypeal margin. Scape length 2.1 mm (2.1–2.2 mm), midlength width 0.33 mm (0.32–0.33 mm), apical width 0.41 mm (0.41–0.42 mm); pedicel length 0.30 mm (0.28–0.30 mm), flagellum length 3.8 mm (3.8–4.0 mm), width 0.40 mm (0.38–0.42 mm), flagellomere I length 0.45 mm (0.45–0.46 mm), flagellomere II length 0.32 mm (0.32–0.33 mm); distance between antennal torulus and compound eye 0.75 mm (0.75–0.81 mm), with punctures small and dense in respect to those of frons; torulus width 0.50 mm (0.49–



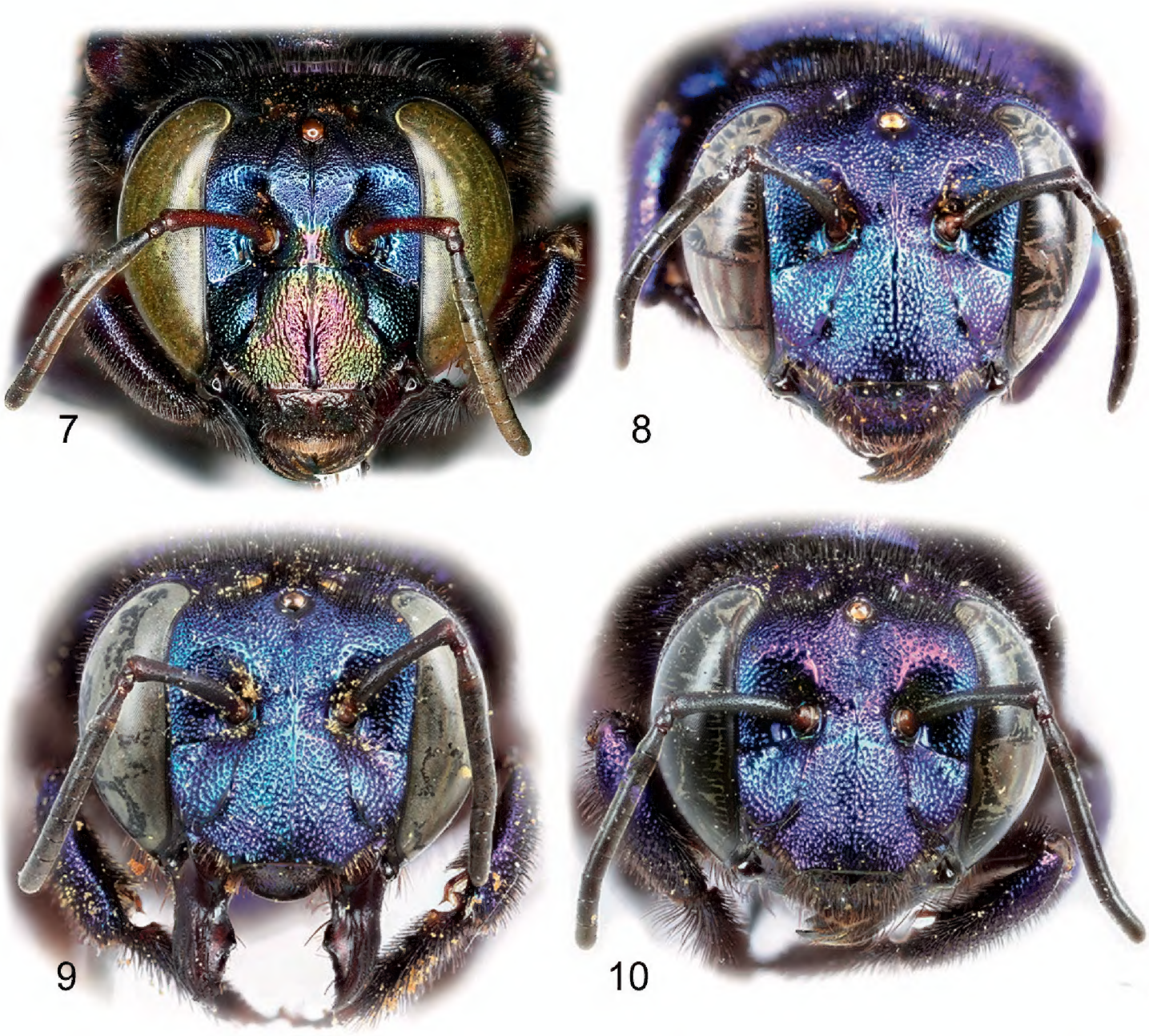
Figures 3–5. *Eufriesea insularis* sp. nov., female **3** dorsal habitus **4** prolateral surfaces of metatibia and metabasitarsus **5** metasomal terga, showing punctation and color of pubescence.

0.51 mm), distance between antennal toruli 1.18 mm (1.18–1.21 mm). Ocellocular distance 0.60 mm (0.60–0.62 mm), ocellocular area impunctate; posterior distance between lateral ocelli 0.85 mm (0.85–0.93 mm), distance between medial and lateral ocelli 0.37 mm (0.37–0.44 mm), width of medial ocellus 0.40 mm (0.40–0.41 mm); interocellar furrow (*sensu* Engel 1999) and postocellar furrow present; integument between posterior ocellus and vertex with punctures denser in respect to frons. Gena with small punctures distinctly separated by shiny integument; gena width 1.10 mm (1.07–1.10 mm) at midlength of compound eye; vertex slightly elevated in facial view

Figure 6. *Eufriesea insularis* sp. nov., female, dorsal view of mesoscutum and mesoscutellum.

in respect to upper tangent of compound eyes. Mesoscutum width 5.5 mm (anterior inter-tegular distance) (5.5–5.7 mm), length 4.9 mm (4.9–5.1 mm); mesoscutum and mesoscutellum with dense punctation, punctures separated by less than a puncture width (Fig. 6), integument between punctures smooth and shiny; tegula with small and uniform punctation, although with some larger punctures along mesal margins, mesal margin demarcated by narrow furrow; mesoscutellum width 4.6 mm (4.3–4.7 mm), length 2.8 mm (2.8–3.0 mm); mesoscutellum slightly rounded in profile, with exceptionally weak medial depression, posterolateral angles rounded; propodeum posterior surface generally smooth, with only fine setigerous punctures; forewing length 15.2 mm (15.1–15.2 mm), width 4.8 mm (4.8–5.1 mm); jugal comb present at base of hind wing, setae of jugal comb longer than width of jugal lobe; distal area of hind wing homogeneously papillate. Metatibia medial length 5.9 mm (5.4–5.9 mm), width 2.8 mm (2.8–3.0 mm); metabasitarsus length on posterior margin 2.7 mm (2.7–3.0 mm), width at base 1.4 mm (1.3–1.6 mm). TI with punctures larger than those of remaining terga, with posterior marginal zone impunctate and longer than those of remaining terga; TII–IV with small, homogeneous punctation, distance between punctures similar to their diameter; TV–VI with punctation denser than on preceding terga; TII–IV with marginal zones short, narrow, impunctate (Fig. 5).

Integument generally dark metallic blue, with purplish hues (Fig. 2); mandible largely black; labrum and clypeus with metallic green, darker on former, and medially with purple iridescence, discal area mostly purple; supraclypeal area as on clypeus (Fig. 7); paraocular area and frons dark metallic blue; antenna dark reddish brown; flagellum



Figures 7–10. Female facial views of representative species of the *coerulescens* species group of *Eufriesea* Cockerell **7** *Eufriesea insularis* sp. nov. (note the prominent mediolongitudinal ridge on the clypeus, unique among these species) **8** *E. oliveri* Gonzalez and Griswold **9** *E. barthelli* Gonzalez and Griswold **10** *E. micheneri* Ayala and Engel.

dark brown to nearly black; gena and vertex with purple and yellowish iridescence; pronotum dark brown except dark metallic blue anteriorly; mes- and metepisterna dark metallic blue, with some purplish highlights; mesoscutum and mesoscutellum dark metallic blue with purple iridescence, but lateral margins of mesoscutum, axilla, and mesoscutellum dark brown to nearly black, without prominent highlights; propodeum dark metallic blue but more brown on posterior surface. Wings with veins dark brown, nearly black in some places, membranes hyaline and darkly infumate (Fig. 3), darker in costal cell, along anterior margin of marginal cell, and somewhat in first submarginal cell; second medial cell with distinct lighter patch (Fig. 3). Femora and tibiae dark reddish brown, with dark blue to purplish iridescence; probasitarsus and tarsi black; metafemur, metatibia, and metabasitarsus dark reddish brown to nearly black, darker on retrodorsal margin of metatibia (Fig. 4). Metasomal terga and sterna dark brown with dark blue, purplish, and greenish iridescence, posterior marginal zones brown to dark brown.

In general, pubescence dark, nearly black; setae particularly dense anteriorly on mesoscutum; abundant and uniform setae on mes- and metepisterna (Fig. 2). Metasomal terga IV–VI with yellowish pubescence in paratype (Fig. 5), black in holotype (Fig. 2); sterna with black pubescence.

♂: Unknown.

Holotype. ♀, México: Nayarit, Isla María Madre, Campamento 21 de marzo, 2-XII-1986 [2 December 1986], V. Melendez (IBUNAM, RA 392).

Paratypes. 1♀, same data as holotype but collected by L. Cervantes (IBUNAM, RA 1014). 2♀♀, same locality as holotype but collected X-1995 [October 1995] by I. Cuedriello (CUCSUR).

Etymology. The specific epithet is the Latin adjective *īnsulāris*, meaning, "of or pertaining to an island", and refers to the restricted distribution of this species on the Islas Marías.

Distribution. This species is known only from Isla Maria Madre, Nayarit State, México. This is the only species of the genus known from an island in the Pacific Ocean. The vegetation on the Islas Marías islands is primarily tropical dry forest, but a good part of the island has scrub, while the denser and higher arboreal vegetation is concentrated in canyons (CONANP 2021).

Discussion

In the key to the Mexican species of *Eufriesea* of Gonzalez et al. (2017), the female of *E. insularis* runs to couplet 3(2) because of its concolorous body coloration and glossa reaching the second metasomal sternum. In that couplet, it would run to *E. oliveri* because of the mesoscutellum with a weak medial longitudinal groove and without the row of dense setae. However, it can be easily separated from that species, as well as any other of the group, by the dark color of the body integument and pilosity, including setae on the sterna. The clypeus has distinct green and purple hues and a strong elevated ridge along the midline (Fig. 7) not present in any other species of the group. In the female of *E. oliveri* the integument is blue throughout with purple hues, and the setae on the metasoma are off-white intermixed with black. In addition, the posterior subapical projection of the metatibial proventral surface is more acutely pronounced than in *E. oliveri* (*cf.* figs. 7 and 33 of Gonzalez et al. 2017).

Proposing a new species based on a limited number of specimens is not ideal as one has a limited (or no) perspective on potential variation, but it is at times still necessary and justified, particularly for exceptionally distinctive taxa. In the current instance, the new species is morphologically distinct and reliably recognized from all other species of the *coerulescens* group. It is likely that *E. oliveri* is the closest relative to *E. insularis* given the morphological similarity between them and the type of habitats they inhabit (dry forests). Other species of the *coerulescens* group exhibit a different combination of features and inhabit different vegetation types, such as *E. micheneri*, which is found in pine forests and other mountainous environments (Gonzalez et al. 2017). Molecular analyses are necessary to explore the relationship of *E. insularis* with the other species of the group, as well as to infer the time of separation between these lineages. The lithologies of Isla María

Madre strongly resemble that of the Jurassic-Cretaceous plutonic and metamorphic rocks found in the Los Cabos Block of Baja California Sur and rocks from the Mexican continental margin between Sinaloa and Jalisco. Thus, the Islas Marías are fragments of the Baja California Peninsula that separated from the mainland of México (Pompa-Mera et al. 2013), all of which suggests a relatively recent arrival of this orchid bee to the islands.

The captured specimens of *E. insularis* are not associated with floral records. However, considering the host plants recorded for other species of the *coerulescens* group that occur along the coast of the states of Jalisco and Nayarit, it is likely that *E. insularis* visits the following plants that are present on Islas Marías as indicated by iNaturalist records: *Cascabela ovata* (Cav.) Lippold, *Tabernaemontana amygdalifolia* Jacq. (Apocynaceae), *Astianthus viminalis* (Kunth) Baill., *Handroanthus impetiginosus* (Mart. ex DC.) Mattos, *Tecoma stans* (L.) Juss. ex Kunth (Bignoniaceae), *Ipomoea hederacea* Jacq. (Convolvulaceae), *Senna pallida* (Vahl) H.S.Irwin & Barneby, *Canavalia rosea* (Sw.) DC., *Indigofera australis* Willd. (Fabaceae), *Salvia apiana* Jeps. (Lamiaceae), *Encyclia parviflora* (Regel) Withner, *Laelia aurea* A.V.Navarro (Orchidaceae), *Antigonon leptopus* Hook. & Am. (Polygonaeceae). However, aside from *S. pallida*, which species of this group frequently buzz pollinate, it would be difficult to determine other sources of pollen and from which plants the males would obtain fragrances, as there are few species of orchids present on the islands. Based on the time of collection, *E. insularis* appears to be active during the rainy season (July to November), and until the beginning of winter. Admittedly, we have only two dates of collection but considering that two of the type specimens have heavily damaged wings we may presume that they began activity months prior, during the rainy season. We hope this contribution encourages further studies to explore the biology and phylogeography of this unique insular pollinator.

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References

Ayala R, Engel MS (2008) A new species of *Eufriesea* from Jalisco, México, with a key to Mexican species of the genus (Hymenoptera: Apidae). Beiträge zur Entomologie 58(2): 227–237. https://doi.org/10.21248/contrib.entomol.58.2.227-237

Cockerell TDA (1908) Notes on the bee-genus *Exaerete*. Psyche 15(2): 41–42. https://doi.org/10.1155/1908/10750

CONANP [Comisión Nacional de Áreas Naturales Protegidas] (2021) Programa de Conservación y Manejo Reserva de la Biosfera Islas Marías. Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT], México, 220 pp. https://www.conanp.gob.mx/que_hacemos/pdf/programas_manejo/IslasMarias.pdf

Dressler RL (1967) Why do euglossine bees visit orchid flowers? Atas Simpósio sôbre a Biota Amazónica (Zoología) 5: 171–180.

Dressler RL (1968a) Observations on orchids and euglossine bees in Panama and Costa Rica. Revista de Biología Tropical 15(1): 143–183.

Dressler RL (1968b) Pollination by euglossine bees. Evolution 22(1): 202–210. https://doi.org/10.2307/2406664

Engel MS (1999) The first fossil *Euglossa* and phylogeny of the orchid bees (Hymenoptera: Apidae; Euglossini). American Museum Novitates 3272: 1–14. http://hdl.handle.net/2246/3046

Engel MS (2001) A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). Bulletin of the American Museum of Natural History 259: 1–192. https://doi.org/10.1206/0003-0090(2001)259<0001:AMOTBA>2.0.CO;2

Engel MS, Herhold HW, Davis SR, Wang B, Thomas JC (2021) Stingless bees in Miocene amber of southeastern China (Hymenoptera: Apidae). Journal of Melittology 105: 1–83. https://doi.org/10.17161/jom.i105.15734

Gonzalez VH, Griswold T, Simões M (2017) On the identity of the adventive species of *Eufriesea* Cockerell in the USA: systematics and potential distribution of the *coerulescens* species group (Hymenoptera, Apidae). Journal of Hymenoptera Research 55: 55–105. https://doi.org/10.3897/jhr.55.12209

Griswold T, Herndon JD, Gonzalez VH (2015) First record of the orchid bee genus *Eufriesea* Cockerell (Hymenoptera: Apidae: Euglossini) in the United States. Zootaxa 3957(3): 342–346. https://doi.org/10.11646/zootaxa.3957.3.7

Kimsey LS (1980) The behaviour of male orchid bees (Apidae, Hymenoptera, Insecta) and the question of leks. Animal Behaviour 28(4): 996–1004. https://doi.org/10.1016/S0003-3472(80)80088-1

Kimsey LS (1982) Systematics of bees of the genus *Eufriesea* (Hymenoptera, Apidae). University of California Publications in Entomology 95: 1–125.

Michener CD (2007) The Bees of the World [2nd edn.]. Johns Hopkins University Press, Baltimore, MD, [xvi+[i]+]953 pp. [+20 pls.]

Moure JS (1965) Some new species of euglossine bees (Hymenoptera: Apidae). Journal of the Kansas Entomological Society 38(3): 266–277.

Pompa-Mera V, Schaaf P, Hernández-Treviño T, Weber B, Solís-Pichardo G, Villanueva-Lascurain D, Layer P (2013) Geology, geochronology, and geochemistry of Isla María Madre, Nayarit, Mexico. Revista Mexicana de Ciencias Geológicas 30(1): 1–23. http://www.scielo.org.mx/scielo.php?script=sci_arttext&pid=S1026-87742013000100001

Ramírez S, Dressler RL, Ospina M (2002) Abejas euglosinas (Hymenoptera: Apidae) de la Región Neotropical: Listado de especies con notas sobre su biología. Biota Colombiana 3(1): 7–118. http://revistas.humboldt.org.co/index.php/biota/article/view/108

Roubik DW, Hanson PE (2004) Abejas de Orquídeas de la América Tropical: Biología y Guía de Campo. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, 370 pp.